A STATISTICAL STUDY OF THE RATTLESNAKES

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VII THE RATTLE, Part 1

Introduction

The rattle is the peculiar attribute of the group of snakes of the New World which are the subject of this study. This remarkable appendage, whose purpose has been a matter of speculation and controversy since these snakes were first observed with astonishment approaching incredulity by European naturalists, offers interesting research problems. For we have in the rattle a mechanism (possibly unique among the vertebrates) which, by the complete separation of successive elements from the body, renders such elements independent of succeeding bodily growth, or other changes short of complete loss or destruction. Hence, if we can determine the chronology of each separation, and the correlation between rattle- and body-size, we have a measure of the rate of bodily growth. The rattle, as corroborative evidence in growth curves, has already been mentioned briefly in this series (Occ. Pap. No. 3, p. 15) but much remains to be added. For the rattle, in both relative size and growth-trend, is found to show definite species differences. There are not only such obvious differences in the comparative sizes of the rattle and the body as that between *Sistrurus catenatus* and *S. miliarius*, but different rattle-growth equations are found in species not greatly different in the adult stage, as, for example, in *Crotalus molossus* and *Crotalus durissus*; for the latter always has smaller rattles when young, but rapidly overtakes *molossus*. Such growth trends sometimes suggest relationships subsequently validated by other characters--for instance that between *C. durissus* and *C. enyo*.

These species comparisons, involving correlations between three variables--body length, rattle number (i.e. position in the string), and rattle dimensions--complicated further by sexual dimorphism, involve a considerable volume of data, too large for a single number of this series, if included with other aspects of the rattle. It therefore appears necessary to delay the presentation of the studies of dimensional differences between species, and to limit the present publication to a discussion of those more general features of the rattle common to all species.

The literature on the rattle is quite extensive; nearly every general work on reptiles mentions rattlesnakes, which inevitably brings in the rattle. There is no pretense that the bibliography at the end of this paper is complete; it is primarily concerned with references devoted to the rattle exclusively, or such as contain a novel or pertinent discussion.

It is not my purpose to review exhaustively the various descriptions and arguments which have been presented respecting the formation and use of the rattle. Rather, I shall emphasize the particular phases of development which appear to me to have received inadequate, and, in some instances, inaccurate treatment. In the classical descriptions of the formation of the rattle, especially those contained in the important papers of Garman (1888 and 1889), there are three items requiring modification or further clarification. These are, first, the character and disposal of the birth-rattle or prebutton; secondly, the relationship between the rattle and the skin; and finally, a modified and more complete description of the intricate mechanism whereby each rattle is slipped backward, yet remains interlocked with its successor, when a new segment has been perfected. But before discussing these features I shall summarize the theories on the purpose of the rattle and my own conclusions.

Purpose of the Rattle and Method of Use

The literature on the rattle is full of speculations upon its purpose; these have been proposed in great variety since the earliest encounters between man and rattlesnake. Some of those which have appeared most frequently conclude that the rattle is used:

- As a mating call
- As a call for help from other rattlers
- To warn other rattlers of danger
- To paralyze prey with fright, or startle them into immobility
- To decoy prey through curiosity
- To charm prey with sound
- To lure prey
    - by imitation of the cicada or other insects
    - by imitation of running water
- As a warning to prey
- As a warning to intruders
    - to avoid injury to the intruder by the rattler
    - to avoid injury to the snake by the intruder
    - to conserve venom and fangs
- To prevent an attack on the tail by insects or carnivores
- As a substitute for hissing
- As a religious warning
- As a venom-carrying weapon

Most of these theories are quite old and have been often repeated; it is difficult to determine with certainty who originated any of them. And both their antiquity and their character indicate that some were proposed by writers who had little opportunity to observe rattlers in the wild, or even under the artificial conditions of captivity. The early compilers of natural histories had to depend on the accounts of travelers in the Americas, or observations on the few specimens which survived the long cold trip to

Europe. So it is not surprising that some of these theories show slight knowledge of rattlesnake habits or their actions under natural conditions, or even of the sound of the rattle; the surprising thing is the continued repetition today of theories and characterizations, many of which do not square with the most elementary observations.

For example, desert rattlesnakes are as well equipped with rattles as any others; yet desert prey would hardly be lured by an imitation of water, nor does the sound of the rattle much resemble that of a gurgling brook. Again, the rattle cannot be considered a substitute for the missing hiss, since rattlesnakes do hiss violently when alarmed.

In considering the many theories which have been suggested to explain the fundamental purpose of the rattle, it is at once apparent that a normal rattlesnake reaction, which is almost universal, gives strong support to one theory as compared to all the others. For what does any rattlesnake do with his rattle? He sounds it when disturbed, as by some movement or the approach of an intruder. Upon this there can be no argument; it is the common experience of everyone who has encountered a rattler in the field or startled one in captivity, unless the snake has become accustomed to humans. I have no desire to assume an irritating attitude of assurance, but certainly I have seen this happen a thousand times; and there are others of far more extensive experience who corroborate this observation.

The rattle is used as a warning signal; upon this, experience permits no argument; if it has other alternative purposes the burden of proof is upon those who advance them, for they are not matters of daily observation. The "Keep Your Distance" use of the rattle is so universal and instinctive that one would suppose this problem of use to have been long since settled; and I might well be accused of giving undue importance to a nonexistent argument, were it not for the fact that books continue to appear, attributing to the rattle as much uncertainty of purpose, or diversity of use, as the popular natural histories of 1800 (e.g. Berridge, 1935; Ditmars, 1936; Gillespie, 1937). And it must be admitted that the nature and purpose of the warning have sometimes been so misinterpreted as to throw the theory into doubt and disrepute.

The warning theory is very old (e.g. Piso, 1648) but from the first it has been, and still is, a matter of argument because of a confusion, often unrecognized, between three types of warning: that is, the warning of (1) intruders, possibly dangerous, warned for the protection of the snake; (2) intruders warned for the protection of the warnee, instead of the warner; or (3) prey, the last being a special case of (2). If we sharply distinguish between these three and point out the manner in which the rattle is beneficial to its possessor, by frightening away creatures which might otherwise injure the snake, we at once eliminate the objections which have been so often advanced against the warning theory. Certainly no animal will warn away the food upon which it depends for subsistence, or develop so intricate a mechanism for the altruistic protection of the innocent passer-by. But it is equally clear that warning devices which tend to safeguard their owners are common in nature; and there is no more reason to question the purpose of the rattle than of these other devices. It is only necessary to show that the rattle is used for this purpose, is often effectual, and that its disadvantages are not as important as have sometimes been supposed.

I shall give no further attention to those arguments against the warning theory which are based on this confusion between a beneficial warning, and one neutral or injurious to the rattler. Darwin himself tried to correct this confusion many years ago, with indifferent success; in fact, his position is still occasionally advanced as an argument against the theory, notwithstanding his clear statement in advocacy of it.*

As I have stated, the validity of the dangerous-enemy warning theory may be presumed to rest with the answers to these questions:

(1) Is the rattle used as a warning?

(2) Is it effective?

(3) Does it ever react against the rattler, and if so, to what extent?

On the first point I think enough has been said already. The rattle is so used--this is the reaction which anyone familiar with these snakes expects invariably when he approaches one.

Is it effective? The answer, of course, depends on the circumstances, as it would were we discussing the growl of a dog, the hiss of a gander, or the earth-pawing of a bull. These are all warning reactions, and they may result in success or failure, depending on the character and purpose of the trespasser. They may be followed by more direct action or by the retreat of the warner.

One of the mistakes made by early writers, and

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* "It is admitted that the rattlesnake has a poison fang for its own defense and for the destruction of its prey; but some authors suppose that at the same time this snake is furnished with a rattle for its own injury, namely, to warn its prey to escape. I would almost as soon believe that the cat curls the end of its tail when preparing to spring, in order to warn the doomed mouse." Origin of Species, Fifth Ed., 1871, p. 196.

As a result of criticism, particularly from St. George Mivart, Darwin clarified the statement in the subsequent edition of the Origin: "Some authors suppose that at the same time it (the rattlesnake) is furnished with a rattle for its own injury, namely, to warn its prey . . . . It is much more probable that the rattlesnake uses its rattle, the cobra expands its frill, and the puff-adder swells whilst hissing so loudly and harshly, in order to alarm the many birds and beasts which are known to attack even the most venomous species. But I have not space here to enlarge on the many ways by which animals endeavor to frighten away their enemies." Origin of Species, Sixth Ed., 1885, p. 162. But even this statement has not prevented his being cited as opposing the warning theory, when, in fact, he opposed only the misinterpretation of enemy warning into prey warning.

repeated in natural histories, is in the general characterization given of the rattler's warning response. Usually the snake is portrayed in his resting coil with rattle sounding. To the possible inadequacy of such a warning mechanism one may agree, but this is not the entire story by any means. Just as the cat arches its back, fluffs its tail, opens its mouth, and spits and squalls, so the rattler has more than a single warning reaction. It is true that a snake found in his resting coil may first sound the rattle without changing position. But if this preliminary warning fails to halt the trespasser he quickly adopts more spectacular methods, which concurrently place him in a better position either for defense or escape. For now, still sounding the rattle furiously, the anterior part of the body is raised above the ground in an S-shaped spiral, with the head and neck held like a poised lance ready for a forward lunge; the posterior part of the body is flattened to stabilize the anchorage or facilitate mobility; and the snake inhales and exhales with a violent hiss.* Meanwhile, in an endeavor better to sense the situation, the tongue is protruded to the fullest extent, and is held alternately pendent and vertically erect, with the tips widespread. Now he is ready for whatever may come; he can strike, if the enemy comes within range, or he can retreat (still facing the intruder) toward the nearest rock or bush which may serve as a refuge.

When a rattle is heard under such circumstances, no prior experience is necessary for a realization of the danger that lies behind it; both the stridency of the sound, and the other actions of the snake to which the sound draws attention, can leave no doubt in the mind of any creature capable of the most elementary reactions of self-protection, that retreat is advisable. Several of the early writers attribute to the noise of the rattle an effect mysterious in its action, in that animals having no previous experience with it--such as the European horse--seem fully aware of its purpose and recoil instinctively from the sound. While the factor of experience may have had some bearing on the genesis of the rattle, as is discussed hereafter, we need no longer consider such experience necessary, especially when this startling sound begins suddenly and unexpectedly under one's very feet. But the effect of the warning is by no means dependent entirely on the initial surprise, so strident is the noise, and so alarming the other actions of the snake.

In judging the effectiveness of this warning as a means of protection, one must have in mind the kinds of carnivores and birds of prey which would seek the rattler as food, and the ungulates which might tread on it fortuitously. Against many of these, such as wolves, coyotes, bobcats, and the like, the rattle would be a valuable protective adjunct--not unfailing, of course, but still of major importance in frightening these creatures into looking elsewhere for a meal. One has only to watch the reaction of a dog or cat with a rattler to see how effective this is, notwithstanding the occasional newspaper stories of rattlesnake killers. And the wild creatures are usually more wary than

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* It is suggested that those who believe rattlers cannot hiss (once the subject of controversy in the pages of a sporting magazine) test this by removing all the loose segments of the rattle, or by binding it up with cloth so that the noise of the breath will not be masked by that of the rattle.

a dog backed by his master. Cowles, 1938, observed that western skunks were driven from customary feeding grounds by the sound of the rattle. Hawks, owls, and ravens would be similarly frightened.

As to the larger herbivorous mammals, they are not usually of such a disposition as to go out of their way in search of trouble. Judging from observations on the reactions of horses and cattle, it is quite evident that the rattle has a definite protective value. In fact, with respect to the ungulates, a specialization of the enemy warning theory has been suggested as indicating the conditions which, coupled with a widespread warning reaction of other snakes--the vibration of the tail when annoyed or alarmed--led to the evolution of the rattle. This theory, which has been accepted by many herpetologists, assumes the ancestors of the rattlers to have lived in a prairie country inhabited by herds of hoofed animals akin to the modern bison. "The hoofs of these ponderous animals, traveling over the plains, must have been distinctly dangerous to snakes living in the open, while the snake's bite would be distinctly unpleasant to the bison, although death would probably have rarely ensued owing to the beast's great bulk. The bison would gladly keep out of the snake's way, however, if warned, and this warning the rattle gave." Barbour, 1934, p. 42. This refinement of the warning theory was suggested by O. P. Hay as early as 1887 (p. 214). It is to be noted that, in the early stages of the development here pictured, recognition of the sound, rather than its alarming stridency, would have been the effective element. But, with the present highly developed instrument, recognition through experience is no longer essential; ungulates are likely to heed the harsh warning of the rattle, preferring, as they do, to avoid disturbance and take a peaceful course.

Garman (1889) describes the transition whereby the rattle probably developed, through the modification and specialization of the conical spine which is the caudal termination of all snakes, but relatively larger and heavier in some than others. The covering of this cone is shed with the rest of the skin. By a gradual enlargement of the cone, a thickening of the covering, with a constriction at its anterior end, and a coördinating middle constriction, the successively-mounted tail cones would be retained in a loose chain, thus producing a sound when the snake vibrated its tail in anger, as is the custom of so many snakes. The culmination of such an evolutionary process would be the present intricate and highly specialized mechanism. Garman also makes the point that the warning serves as a means of conserving venom and fangs, a further advantage to the snake.

Summarizing this phase of the theory, we conclude that the rattle is of definite value when sounded as a warning to animals which, with intention or unconsciously, might injure the snake.

We come now to the third query: Is the rattle ever a detriment by advertising the presence of the rattler to potential enemies, when it might otherwise escape?

A number of the early writers assume that, like the bell on a cow, the sound of the rattle is incidental to any movements of the snake, thus continuously broadcasting its presence. But, as a matter of fact, unless a snake is crawling through rocks or brush, so that the rattle strikes extraneous objects, it makes no sound at all. Even when it is so struck, the click or rasp can be heard only a few feet; it is quite different from the shrill hiss produced when the tail muscles deliberately vibrate the rattle. In fact, it is impossible to simulate the true sound as made by the snake, by rattling a string of rattles by hand, for the necessary speed cannot be attained.

Others have pointed out that the use of the rattle may serve only to invite destruction by certain animals, such as deer and hogs, which are said to kill rattlers upon occasion. For example, Berridge, 1935, considers this a fatal flaw in the warning theory. Now certainly this would be true if the rattle served to invite destruction by advertising the snake's presence, when inconspicuous inactivity, or a silent withdrawal would be the safer policy. This, however, misjudges the rattler's ordinary response to the presence of an intruder. No field collector knows how many rattlers he may pass, which escape merely by lying quiet. But I have spied enough of them, fully aware of my presence, yet making no sound or movement, to realize that they will depend on this method of escape whenever possible. The rattle is the reaction of a suddenly startled snake, or one which thinks its presence to have been discovered and proceeds to use the warning as a last resort (short of the strike), in the hope of frightening the trespasser away.*

I think this criticism also misjudges the reaction of animals to the sound of the rattle. They are pictured as saying to themselves when they hear it, as a man would, "Here is a dangerous creature which I had best destroy, for the safety of others who may pass this way." But no wild animal would reason thus; there is always a more specific purpose in attack, such as a desire for food, or the protection of young. Against such creatures, keeping in mind the fact that the rattle is not sounded until procrypsis has failed, its possession is definitely protective.

It is possible that, with man, an enemy who can destroy at a distance without endangering himself, the rattle is a disadvantage. For man is poorly equipped with senses and the rattler may sometimes advertise himself too quickly when he might otherwise lie undiscovered. But this is no valid argument against the warning theory, since rattlers long antedated man in the New World; and the rattle was developed without regard to the novel conditions involved in this addition to the local fauna.ø The same argument holds

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* A defense reaction of a different kind, probably reserved for king snakes and other ophiophagus species, which are immune to venom, and certain forms of skunks, has been described by Cowles, 1938. The rattler raises the mid-section of the body in a bow and strikes downward with it. Even very young rattlers exhibit this reaction in the presence of a king snake.

ø Under certain circumstances the snake's use of the rattle has been an aid to collectors. Thus J. R. Slevin located specimens of C. l. klauberi in the Huachuca Mountains, Arizona, by rapping on stones on talus slides, which caused many snakes underneath to sound their rattles, and disclose their whereabouts. The same scheme was used by the Hancock Expedition on Tortuga Island. Once I had the experience of having a pyrrhus rattle at my car as it passed the pile of rocks in which he was hidden.

in the case of the domestic hog and goat.

We may thus summarize our conclusions with respect to the warning theory: The rattle is used as a warning; it is often effective; detrimental results are rare, particularly in the case of the indigenous fauna.

We now pass to some of the other uses of the rattle which have been suggested and examine the evidence for such uses, and the arguments with respect to them. Of these the prey lure, the mating call, and the call for help have been the most persistently advanced.

The experiences cited in the literature to authenticate them have been few and the evidence usually conflicting, or subject to diverse interpretations (Dudley, 1723; Shaler, 1872; Aughey, 1873).

My own field experiences and those of my associates in this vicinity, have been completely negative. Certainly the best argument against the mating call theory is the absence of rattling sounds in rattlesnake infested areas during the mating season, or when snakes mate in captivity. Further, it is to be noted that young rattlers rattle vigorously long before the acquisition of a second rattle makes the vibration audible. This early use (immediately after birth, in fact) is hardly to be explained as a sex call.

The same reasoning holds with all relationships between the rattle and prey; if such were the purpose, snakes would often be heard rattling in the rocks and brush, especially in the spring; but they are not, except when there is some source of disturbance to alarm them. The lure theory is particularly difficult to justify on a practical basis, having in mind the diversity of foods upon which the different species of rattlers subsist, including a great variety of mammals, birds, and lizards. It is hard to conceive what kind of sound would act as a decoy, a lure by imitation, or a charm, for so diversified a lot of creatures.

The experiments of Manning, 1923, tend to prove that the rattlers' audient range does not permit their hearing the sound of the rattle. This, if verified, would at once eliminate the mating and call-for-help theories, or any others depending on recognition of the sound by other rattlesnakes.

I have noticed occasionally, when a number of nervous rattlers were kept in separate boxes, that excitement upon the part of one sometimes started others rattling, but the vibrations may have been transmitted through the floor rather than the air. Or the artificial conditions incident to the boxes may have caused an increase in audibility or a change in frequency.

In any case, there is little evidence favoring the call-for-help theory. On several occasions in the field I have come upon two or three rattlers together. One, alarmed at the intruder might rear up and rattle violently, yet the others either did not hear the sound or appeared unimpressed by it.

C. B. Perkins has observed that a rattler in captivity will sometimes rattle when a second snake approaches food which the first has struck or is eating. This is a rather natural extension of the warning, like the growl of a dog, and shows that rattlers do not change the primary purpose of the rattle when using it on their fellows. And certainly, if we concede that the rattle has at least a partial use as a warning, we have difficulty, from a psychological standpoint, in justifying the other uses. It is hardly conceivable that a creature of so low an order of intelligence as the rattler, would instinctively use the same reaction as a threat to enemies and a mating call; or as a warning and a lure for prey. Rattlers are equipped with the same sense organs and special scents as are possessed by other snakes; these are presumed to serve to bring the sexes together in the mating season.* J. D. Mitchell, 1903, states that male rattlers are aggressive in the mating season and will promptly rattle to challenge any intruder. This may have given rise to the mating-call theory.

Warning devices or mechanisms are relatively common and of considerable diversity among snakes--for example, the hiss of the gopher snake, the spreading hood of the cobra, the scraping scales of the saw-scaled viper, and the inverted tail-spiral of the ring-necked snakes. But the most widespread is the vibration of the tail as a sign of alarm or annoyance. This ancient and extensively used reaction is generally interpreted as a warning mechanism; and there seems no more reason to question the purpose of its more highly specialized descendant, the rattle of the rattlesnake. Although a harmless snake, vibrating its tail amongst dried leaves, can simulate the noise of a rattler quite effectively, this cannot be construed as imitative; the vibration of the tail antedates the rattle and, besides, is widespread in the Old World, where rattlers do not occur.

It may be noted that at least one rattler (_C. stejnegeri_) has a rattle so tiny that it must be virtually inaudible. This rattler comes from a remote region in northwestern Mexico and I have had no opportunity to observe a live specimen, or to hear the rattle in use. In the adults the rings are barely 3 mm. across as compared with over 20 mm. in some large species. The tail is proportionately much longer than in other rattlers and is more tapered at the end. It has been suggested that this rattler is reaching the opposite end of evolution from the primitive creatures which first warned the bison, and is now losing its rattle.

Does a rattler always rattle before striking? Certainly not; if a snake be stepped on he will turn and bite with no coil, rattle, or any pause or warning. A snake closely approached may be so suddenly alarmed that he will lunge at the intruder with a simultaneous sound of the rattle; or he may omit rattling entirely. But the threatening rattle, as the initial step, is the more usual procedure. Sometimes a snake will endeavor to seek a nearby retreat, either facing his enemy and with forebody raised in the striking pose, or more precipitately by the usual crawling method; in the latter case he may stop rattling, thus abandoning his warning threat for simple escape. If escape be denied he will always coil and threaten; I have yet to see a rattler, not already intimidated by captivity, which, when cornered, would not turn and face the intruder, with rattle sounding furiously

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* Noble, 1937

and with the forebody poised for a strike.

As has been stated, rattlers discovered in the resting coil will sometimes sound the rattle without change of position, until a nearer approach of the enemy causes them to shift to the defensive or striking coil. Occasionally they will give a characteristic warning click or two of the rattle before sounding it continuously. If first found in the ordinary crawling posture, a rattler will usually draw itself up directly into the striking coil if the intruder is quite close. If it desires, a rattler can sound the rattle while crawling.

To conclude: The threatening pose of the rattler is aided by the rattle in two ways; the stridency of the sound is in itself alarming; and attention is drawn by the sound to a creature, which by every detail of deportment, indicates the danger of nearer approach. There is very positive evidence for the warning theory of use, but little or no evidence for the others which have been proposed.

Character of the Sound

Many are the similes found in the literature for the sound of the rattle: The buzzing of bumble bees or other insects, peas shaken in a gourd, wheat rattled in the hand, escaping steam, the cicada, running water, rustling leaves, a child's rattle, an alarm clock, the folding of dried parchment, the whirring of many spinning wheels, blowing through loose lips, the rattling of seed pots, the wind in the trees, the hissing of a hard rain. Of these probably the most accurate likenesses to the noise made by a large rattler are the sounds of certain species of cicada, and the hissing of steam through a small jet.

The term "rattle" is to a certain degree a misnomer when applied to the noise made by the snake; for "rattle", by definition, implies discontinuous or discrete sounds, whereas the separate sounds emanating from a snake's rattle are much too close together to be distinguished by the human ear. The result is a toneless* buzz, or, in the case of the larger snakes, a loud hiss. The distance at which it is audible depends on the kind and size of the snake--from only a few feet in the case of _S. miliarius_ to 200 feet or more with large specimens of such species as _C. adamanteus_, _C. durissus_, or _C. cinereous_. When water-soaked the rattle is practically inaudible. However, it is not permanently affected by moisture, and recovers its audibility as soon as dry.

Method of Vibration

As will be discussed hereafter, the rattle is elliptical or subrectangular in cross-section, with the longer axis vertically perpendicular to the center line of the body. In the crawling position the rattle is tipped up to avoid wearing on the ground. When coiled for defense, with the rattle sounding, the tail and rattle are held in a position approaching the vertical, or with a posterior slant.

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* That is, dry and rasping, without hum, ring, or the quality of metallic vibration. It is not toneless in lacking a substantially constant frequency.

In this position of almost perfect balance, it will deliver the maximum noise for a given expenditure of energy and with the least wear.

The vibration is transverse or lateral, that is, in the direction of the shorter axis of the subrectangular section, or horizontally at right angles to the center line of the tail.

Through the courtesy of Dr. Phillips Thomas and Mr. A. E. Hitchener, of the Westinghouse Electric and Manufacturing Company, I was able to watch the operation of the rattle under the light of a variable-frequency neon stroboscope. We had available a pair of C. tortugensis, with the long rattle strings characteristic of this island species, one of 13 and the other 11 rattles. It was most interesting to see our previous assumptions concerning the nature of the vibration borne out in this visual test. With the stroboscope light regulated to a frequency just below that of the snake's tail, the waves could be clearly seen going out from the tail to the end of the rattle string. The amplitude increases as the wave moves outward, because of the cumulative looseness of the interlock. The wave is much like that which may be sent along a loose rope.

By moving the segments of a rattle slowly, with a transverse motion similar to that seen under the stroboscopic light, the method whereby the sound is produced may be observed. Between each lobe of each segment, and the interlocking lobe of the segment within, a succession of contacts and separations is produced, especially on the deep groove surfaces. No doubt each pair clashes at a number of different points, so that several distinct sounds are produced, as the wave passes each lobe. The total number of sounds per cycle equals twice the number of rings multiplied by the contacts per ring. Assuming only one contact per ring, three lobes per segment, and a 6-rattle string, at 50 cycles per second (an approximate average number), we have 1000 contacts per second. It is obvious that a frequency such as this will result in a hiss rather than discrete sounds. A young rattler with only two rattles makes about 100 contacts per second; the result is a much softer buzz than the hiss of an adult. Since the rattle is hollow, dry, and the material somewhat pliable, like heavy parchment, the sound is unmetallic; it seems to have no musical quality.

In addition to the ordinary high-speed vibratory motion, the snake, while rattling, often waves the tail slowly from side to side.

Speed of Vibration

For the study of the vibration of the rattle, a simple kymograph, driven by a synchronous motor on a controlled-frequency circuit, was employed, with stylograph paper on the drum. For registration a pin was run vertically through the proximal segment of the rattle, the point inserted downward between the rattle shell and the flesh of the tail tip. The snake was held with the neck in the left hand and the posterior part of the body in the right. The vibrating tail was then lowered until the pin touched the kymograph drum. As it was later found that the speed of vibration was characteristic of each snake, and its condition and disposition, rather than the weight of the rattle string, it is believed that the pin weight did not affect the result. Similarly, as the scratch on the waxed surface was usually so fine as to require a magnifier for its examination, the drag of the pin is not thought to have been a source of serious error.

Altogether, 173 records were made on 81 snakes of 20 different species and subspecies. It was found possible to get good records in most cases when large specimens not long in captivity were used. The juveniles of the large species, or adult snakes of the smaller forms, did not produce legible records. Specimens long in captivity seldom reacted efficiently; and even fresh specimens often refused to rattle properly, after being held for a few moments, in spite of being vigorously pinched.

Although I suspect that there may be some specific differences in rattle speed--the longer tailed forms, such as C. d. durissus, vibrating their tails at a slower rate than C. v. oreganus, for example--I soon gave up any hope of proving this statistically, for various other conditions, such as the temperature and the degree of anger or fear evidenced by the snake, make such wide variations as to mask completely any species differences.

The kymograph records indicate that, for each snake, under specific conditions, the rattle reaches full or characteristic speed within a few cycles--there is no gradual coming up to speed. The same conclusion is reached from observing snakes making the spasmodic or nervous clicks with which they often begin or end a sound of the rattle; these are really short runs of the rattle at full speed. However, there are occasional variations within short ranges. For example, a specimen of C. m. stephensi changed from a speed of 54 cycles per second to 45 within two cycles.

The tail vibration seems closely to follow simple harmonic motion. To amplify the kymograph record a needle was run longitudinally down the center of the long rattle string of a large snake, thus making it a rigid, but light, extension of the tail. The end of the needle was allowed to touch the kymograph drum and the resultant curves were photographically enlarged. The wave was analyzed as a Fourier series by the twelve coördinate method, with the following result:

$$\begin{aligned} y = 180.4\ &(x + 92.58^\circ) + 6.4\ (3x + 61.8^\circ) \\ &+ 5.3\ (5x - 176.7^\circ) + 1.9\ (7x + 152.1^\circ) \\ &+ 0.8\ (9x + 50.2^\circ) + 0.8\ (11x - 172.9^\circ) \end{aligned}$$

This is not presumed to be highly accurate, owing to the unnatural effect of the needle; but as the third and fifth harmonics have an amplitude of only about three per cent of the fundamental, and the higher harmonics one per cent or less, the curve closely approaches a pure sine wave, and simple harmonic motion is indicated.

I have stated that the wave, as seen under stroboscopic light, gains in amplitude as it travels out toward the end of the rattle, because of the cumulative looseness of articulation. Near the tip of the tail itself the amplitude is quite small--hardly more than a millimeter or so on each side of the center line--even in a large snake. A young C. adamanteus 830 mm. long, vibrating its tail at the rate of 51 cycles per second, had an unusually large amplitude; this was measured and found to be 3.4 mm. from right to left peak, or a motion of about 1.7 mm. on each side of the center line. This is certainly greater than the average motion, which, in a snake a yard or so long, is found seldom to exceed 2 mm. between extremes, and is usually between 1 mm. and 1-1/2 mm. But the rattle itself, particularly at the outer end, has a far greater motion because of its looseness.

The proximal rattle, through which the motion is transmitted to the remaining segments of the string, is rather closely attached to the forming matrix subsequently to be described. The terminal caudal bones are coösified into a central reinforcement within the matrix; this forms a short shaker (Fig. 47). The muscles producing the motion are in the posterior part of the tail but anterior to the matrix; there are six bundles of these, three on each side. While the amplitude of the motion is not great, the muscles are powerful and are capable of maintaining the vibration at full speed for a considerable time.

A study of kymograph records indicates that under constant temperature conditions, if there be a change in speed there is likely to be a change in amplitude as well; a lower frequency accompanies a lower amplitude.

An elementary test is sufficient to prove the important effect of the temperature on the speed of vibration. Eight runs on 5 specimens of C. v. viridis from South Dakota at a temperature of 52° F. produced an average rattle speed of 41.0 cycles per second (max. 44.9, min. 28.1); ten tests on 6 specimens at 73° F. an average speed of 57.9 cycles (max. 66.9, min. 53.2). Thus an increase of 21° F. raised the speed about 41 per cent.

The weight of the rattle seems to have no important bearing on the speed, as shown by the following tests in which segments were successively removed from the strings:

Female Nebraska C. v. viridis 980 mm. long:

Rattles in String	Speed, Cycles per Second
6	45.5
4	51.5
2	50.8
1	50.2

Female Nebraska C. v. viridis 820 mm. long:

Rattles in String	Speed, Cycles per Second
7	47.6
5	48.3
3	46.0
1	47.8

Only in one case was there an increase in the speed when rattles were removed, and this may have been the result of an increase in temperature from exertion.

There seems to be no appreciable sexual dimorphism; nor was I able to find any consistent trend of rattle speed with size. Of course, it is to be remembered that no successful tests were made on juveniles or adolescents; such a study could be made accurately only with a calibrated variable-speed stroboscope. Of the species tested, at temperatures of from 65° to 75° F. (C. d. durissus, C. basiliscus, C. enyo, C. m. molossus, C. cinereous, C. lucasensis, C. ruber, C. exsul, C. v. viridis, C. v. abyssus, C. v. lutosus, C. v. oreganus, C. m. pyrrhus, C. m. stephensi, C. l. lepidus and C. l. klauberi)it was seldom that the speed was above 60 or below 40 cycles per second, with an average of about 48 cycles.

The lowest speed recorded was 28.1 cycles at 52°, and the highest 66.9 at 73° F., both in C. v. viridis. No tests were made at temperatures above 78° F.

To determine the amount of fluctuation in speed in a continuous sounding of the rattle, I measured the lengths of successive cycles and secured the following: Total cycles 147; mean speed 46.09, maximum 52.6, minimum 41.7, interquartile range 44.67 to 47.64 cycles per second; coefficient of variation 4.82 per cent. Probably the true variations are somewhat less than these figures since the method of measurement tends to exaggerate the fluctuations. This test was made on a specimen of C. v. viridis at 73° F.

I find nothing to justify the suggestion of Hopley (1882, p. 312) that a snake changes the speed of the rattle deliberately to vary his signals. Besides the important effect of temperature, the fact that a higher amplitude accompanies a higher speed indicates that a greater degree of alarm or anger tends to speed up the rattle. These seem to be the most important factors affecting the vibratory rate.

Annoyed snakes can rattle for very long stretches without interruption. Perry, 1920, mentions a horridus which rattled for one-half hour. I have never made any accurate records of long runs, but I have no doubt they sometimes exceed this period. In the laboratory it is frequently necessary to remove live specimens, so annoying is the continuous rattling of specially nervous snakes not yet accustomed to captivity.

Lengths of Rattle Strings

The lengths and completeness of rattle strings constitute an interesting subject of investigation. However, in gathering such data it is virtually impossible to secure statistics exactly representative of field conditions, since it is inevitable that some rattles will be broken in capturing the specimens, and, unless great care be taken, in their preservation as well. It is not satisfactory to utilize specimens which have been the subject of frequent examination in a museum, for, when the rattles are softened by preservative, they are particularly subject to breakage in removal from the containers. Also, one must be careful not to utilize series of specimens in which there has been any conscious selection with respect to the length and character of the rattle strings. For example, my own collection of C. ruber would give an entirely erroneous idea of the proportion of unbroken rattle strings occurring in that species, since I have deliberately saved specimens with unbroken strings in order to accumulate certain dimensional data. Snakes long in captivity are unsatisfactory as their subjection to frequent disturbance may cause rapid rattle wear, and skin changing periods are likely to be abnormal.

In Tables 31 and 32 data are presented on two large series which were carefully handled in both capture and preservation, and which are believed to be unbiased samples. Only adolescents and adults are included.

In statistics of this character it is necessary to take the season of capture into account as well as the species of snake. The Platteville series was collected about their dens at the time of going into hibernation in autumn or coming out in the spring. At this time it will be observed that most of those with complete strings have 5 rattles. However, had the collection been made in the summer, 7 rattles would have been the mode. By the following hibernating date, were the strings complete, the same snakes would have had 8 or 9 rattles; but, as is seen, few retain such strings entire, for breakage is rapid after there are 8 in the string. Thus, in the table, these older snakes fall into the broken-string group.

Similarly in the lucasensis statistics the table represents an early spring series. Had it been made in the summer, 8 and 9 rattle strings would have dominated the complete strings. By the following spring these would become tens or elevens. But unbroken strings of this length are unstable, so that when next spring does arrive, few, if any, of the two and a half year old snakes still have unbroken strings, and the 7 rattles of the one and a half year old snakes of one year later would still set the mode at this figure.*

Although the season of collection affects the mode of the complete strings, it is less likely to affect broken strings. For, if a rattler gets 4 new rattles per year, it is obvious that the modes in complete strings at any season will be four units apart. But breakage occurs irregularly and once a string is broken the seasonal modes or peaks should largely disappear.

That there is some sexual dimorphism in the retention of complete strings is evident from the tables. For example, 30.5 per cent of the male viridis had complete strings, while 43.1 per cent of the female strings were entire. This difference, by the use of a four-fold contingency table, is found to be significant. In the lucasensis the corresponding percentages are 12.6 per cent for the males, and 17.6 per cent for the females. I am of the opinion that the higher breakage shown by the males results from the same cause as the predominance of males in collections, namely, their greater activity.

The lower percentage of unbroken strings in lucasensis, as compared with viridis, is a climatic effect. For lucasensis has a longer growing season and averages about 7 rattles (if the string is complete) in the early spring, as compared to 5 in viridis. But a 7-segment string has a lower chance of survival without breakage than a 5-segment, other conditions being equal.

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* See Occ. Pap. No. 3, fig. 3, p. 16, for the correlation of age with rattle segments in a typical species.

TABLE 31

PLATTEVILLE SERIES OF *C. v. viridis*

Number of Rattles	Complete Strings			Broken Strings			Total		
	M	F	T	M	F	T	M	F	T
0				2	3	5	2	3	5
1				1	6	7	1	6	7
2				6	9	15	6	9	15
3	1	1	2	15	17	32	16	18	34
4	10	21	31	53	33	86	63	54	117
5	69	69	138	53	42	95	122	111	233
6	8	20	28	46	37	83	54	57	111
7	9	12	21	43	12	55	52	24	76
8	4	2	6	8	5	13	12	7	19
9				2	1	3	2	1	3
10				1		1	1		1
Total	101	125	226	230	165	395	331	290	621

(M, male; F, female; T, sexes combined)

TABLE 32

CAPE SERIES OF *C. lucasensis*

Number of Rattles	Complete Strings			Broken Strings			Total		
	M	F	T	M	F	T	M	F	T
0									
1				1		1	1		1
2				2	3	5	2	3	5
3				2	3	5	2	3	5
4				3	4	7	3	4	7
5	1	3	4	10	9	19	11	12	23
6	6	6	12	15	21	36	21	27	48
7	9	7	16	31	17	48	40	24	64
8	6	5	11	38	17	55	44	22	66
9		1	1	28	14	42	28	15	43
10	2		2	22	7	29	24	7	31
11				15	4	19	15	4	19
12					1	1		1	1
13					2	2		2	2
14					1	1		1	1
Total	24	22	46	167	103	270	191	125	316

(M, male; F, female; T, sexes combined)

At this point mention should be made of the fact that the button, being the thinnest and most fragile of the rattles, and having only one gripping edge, is the most easily lost (Table 33). The subsequent rattles are successively strengthened, both by thicker and better reinforced walls; and, because, beginning with rattle No. 3 or No. 4, the second transverse groove is serviceable in gripping the succeeding rattle, so that the hold is doubled. At about rattle No. 8 almost full adult strength and holding power are reached (see p. 41). This fragility of the early rattles, especially the button and Nos. 2 and 3, makes it clear why extra long strings--say above 11 rattles--are so seldom unbroken strings.

While there is sexual dimorphism in the percentage of specimens having complete strings, there is no significant difference in the average length of the complete strings, the following being the figures:

Average Number of Rattles, Complete Strings

	Males	Females	Both Sexes
Platteville *viridis*	5.25	5.22	5.24
Cape *lucasensis*	7.16	6.78	6.98

Corresponding figures for the broken strings are as follows:

Average Number of Rattles, Broken Strings

	Males	Females	Both Sexes
Platteville *viridis*	5.24	5.04	5.15
Cape *lucasensis*	7.91	7.27	7.67

Hence, while more females retain complete strings, they do not average more rattles; this indicates slower female growth, or fewer skin changes at a given age.

It will be observed that there is little difference between broken and unbroken strings as far as the average number of rattles is concerned. I would expect to find a somewhat higher average in the broken strings because of the greater strength in the terminal rattles. There is some indication of this in *lucasensis*. It must be recognized that the broken strings are penalized by having among their number several individuals with from 0 to 3 rattles; none with these low numbers is contained in the complete-string category, since they would be juveniles and therefore eliminated from our tabulation. If we begin with 4-rattle strings then, as expected, the broken strings have a higher average number of segments than the unbroken.

One point does stand out in the figures which have been presented--namely, the definitely higher average of the *lucasensis* strings as compared with *viridis*. Differences such as this may be attributed to a variety of reasons: the comparative dispositions of the snakes; the prevalence of enemies causing the use of the rattle; the character of the country inhabited; and, finally, the relative strengths of the strings.

An example of the first differential character may be observed in *C. ruber* and *C. v. oreganus* in San Diego County. In a given period, 21 of the former were secured with complete strings having in excess of 8 rattles; of *oreganus* there were only 12. The total number of adults was about the same in the two species. *Ruber* is probably the most placid of all rattlesnakes; *oreganus*, on the other hand, is of a rather nervous temperament. As these two snakes live in the same surroundings, characterized by boulders and chaparral, it is to be presumed that disposition accounts, at least in part, for the differences in the lengths of the rattle strings.

As examples of the second effect--the prevalence of enemies--the island species *tortugensis* and *exsul* may be cited. The former especially is characterized by long rattle strings. Out of 270 *lucasensis* with broken strings, only 4, or 1.5 per cent, had more than 11 rattles; out of 37 *tortugensis*, 7, or 18.9 per cent, had more than this number, including one with 15, one of the longest natural strings I have seen. Similarly, of the available specimens of *exsul*, 8.7 per cent had more than 11 rattles.

With respect to the character of the country, it has been noted, as might be expected, that snakes which inhabit sandy areas, such as *cinereous*, in some parts of its range, and *cerastes*, are often characterized by long strings. For they are less subject to wear and breakage, than the rattles of the brush and rock dwellers; the latter not only suffer from abrasion, but are more likely to have their rattles caught in a forked branch or the cleft of a rock.

Finally, we have the matter of relative strength. I think it probable that the difference between the average length of *viridis* and *lucasensis* strings, to which attention has already been directed, is largely due to this effect. It is true, of course, that the larger rattles are subject to greater amplitude of vibration and more friction, but they seem to be even more than compensated for these requirements by added thickness and strength. The smaller species, such as *S. miliarius*, *S. catenatus*, *C. lepidus*, and *C. t. pricei*, particularly the first named, rarely have strings, either complete or broken, exceeding 7 or 8 rattles. In general, where the other variables are equal, larger species of rattlers tend to have longer strings. Small rattlesnake species with proportionately large rattles, of which *tigris* is the best example, often have long strings; for, in these, there is an abundance of structural strength, compared to the forces causing breakage.

It is of interest to note that in the Platteville series, several of the effects which I have mentioned militate against long strings. In this series of 621 snakes (adolescents and adults) only a single snake reached ten rattles; this was a broken string on a male snake; there were three snakes with nine. The longest complete strings contained only eight rattles; of these there were six, four males and two females. The correlation of body length with number of rattles, which I hope to discuss in a subsequent paper, indicates that many of these adults would have had strings far exceeding these in number, had they remained unbroken; in other words, it was not a size limitation that cut the long strings to such small numbers--rather, it was the natural wear and breakage.

Very short strings are also abnormal; thus out of 621 Platteville snakes (no juveniles included) five had no rattles, and seven only one. These were noiseless and therefore useless strings. The five unfortunates had had their rattles (including the matrices) cut completely off; they showed by other scars that they had been "killed", and their rattles removed as trophies, but had subsequently recovered.

I have never made a particular effort to secure data on record-breaking strings, and the entirely fantastic figures which have appeared in the popular literature on the subject need little comment, for it is well known that strings can be quite easily pieced together to deceive the unwary. I can only say that, out of some ten thousand rattlesnakes which constitute the bases of these notes, only one (an island _lucasensis_) had as many as sixteen rattles, and only two others (a _cinereous_ and a _tortugensis_) fifteen.* The longest unbroken string was thirteen; this was on a Cape _mitchelli_. Of course, it must be understood that these data are partly the result of studies of preserved specimens, which, in the handling they received, frequently lose rattles. But in any case, strings longer than these, although they no doubt occur, must be highly exceptional.

Often, when too many rattlers are crowded together in a shipping container, their tails and rattles will become so tangled together enroute, that they can be separated with the greatest difficulty, and only then at the expense of much breakage. Whether anything of this kind ever happens in the dens during hibernation I do not know.

However we may regret, from the standpoint of a statistical investigation, the fact that so few long and complete strings of rattles are at hand, we must admit that from the viewpoint of the owner, breakage is both normal and beneficial. Very long strings, say beyond 12 rings, cannot be particularly serviceable from the standpoint of a sound producing apparatus and might be a positive detriment, for the very length and weight would tend to damp out the vibrations. Probably a string of from six to eight rings would constitute the most efficient vibrator. Thus it seems normal that rattles should be worn away, so that the long string is exceptional. Both abrasion by extraneous objects and the vibratory use of the rattle itself are effective in limiting the strings. In any case, it is to be remembered that string averages in the field are certain to be somewhat higher than those in collections because of inevitable breakage in capture, transportation, and preservation.

It has been noted that some snakes suffer considerable wear and breakage of rattles in captivity, particularly if they retain enough animation to rattle at the approach of strangers. Rattlers brought into a zoo with very long strings, soon wear them out and lose many segments. On the other hand, rattlers born in captivity, and therefore accustomed to man, or others which are well treated and become inured to cap-

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* This does not include records of the Wiley brood mentioned on p. 30.

tivity, may develop very long strings without breakage. This indicates that the snake in the wild does not often have cause to sound his rattle for long periods; in fact, in rattlesnake country, one almost never hears a rattle sounded except as the result of one's own intrusion upon the privacy of a snake.

A rattler, detained by holding the rattle, quickly demonstrates how rings are lost in nature, should a rattle be caught in the fissure of a rock or the fork of a twig; for, under such circumstances, the snake will give a violent twitch of the tail and the offending rattle will be snapped off.

To the statements respecting some of the very long strings mentioned in the literature, we must take definite exception. A string of 44 mentioned by an early traveler has been cited unnumbered times by subsequent writers. A string of this length would be broken by kinking or merely by an attempt to pull it out from under the snake's own body. But it may be presumed that this string will persist in future natural histories at least until the last hoop snake has rolled down the hill, to stab, with its venomous tail, the defenseless oak tree at the bottom. The indestrucitibility of folk lore was never better illustrated than in tales regarding the rattle. The story that the rattle is sounded involuntarily, whenever the snake moves, was denied at least as early as 1747 (Mead), yet it still appears occasionally. And that perennial favorite to the effect that the snake adds one rattle to the string annually, giving an accurate record of the snake's age (which would ignore breakage, even if the annual addition were true) was denied by Lacépède as early as 1789, and since then by innumerable other authors. Nevertheless, it is extensively believed today.

Chemical Composition

Chemical analyses made in duplicate, on rattles and substances assumed to be somewhat similar in composition, produced the following average results, all components being expressed as percentages:

	Rattle	Rattlesnake Skin	Cattle Horn	Human Hair
Carbon	47.33	48.17	50.89	48.14
Hydrogen	7.17	6.94	6.72	6.89
Sulphur	1.35	1.13	3.17	4.12
Nitrogen	14.13	13.08	16.66	16.06
Ash	2.53	9.12	0.40	0.74
Difference (Oxygen, etc.)	27.49	21.56	22.16	24.05

All determinations were made on a moisture-free basis.

The high ash content of the skin is notable; it was found to contain iron, calcium, magnesium, aluminum, manganese, potassium, sodium, phosphates, sulphates, chlorides, and silica.

It will be observed that the gross chemical composition of the rattle is not greatly different from that of cattle horn, or human hair. Proportionately the greatest

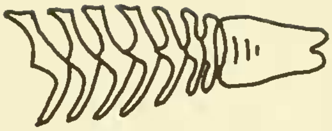

Fig. 47

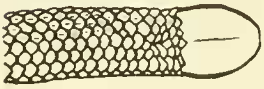

Fig. 48

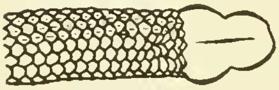

Fig. 49

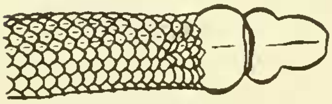

Fig. 50

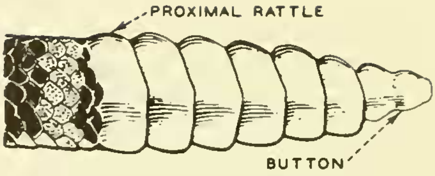

Fig. 51

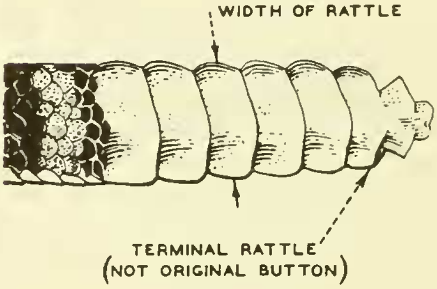

Fig. 52

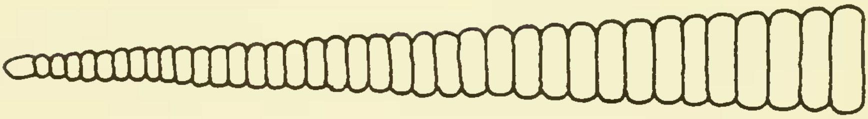

Fig. 53

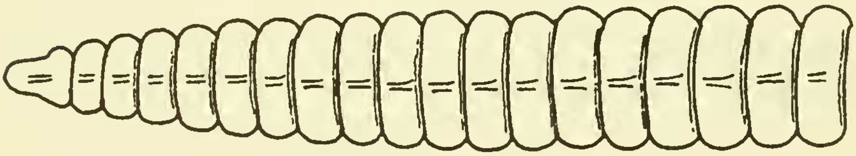

Fig. 54

Fig.47. The shaker within the matrix
" 48. The prebutton
" 49. The button
" 50. The button and No.2 rattle
" 51. Rattle terminology -- complete string
" 52. Rattle terminology -- broken string after loss of several segments
" 53. Trend in rattle growth as shown in early natural histories
" 54. Actual trend in rattle growth (This long unbroken string is shown to illustrate the trend; actually for a snake to retain a string of this length unbroken would be quite phenomenal).

divergences are in the low sulphur and high ash content of the rattle.

These analyses were made through the courtesy of Mr. C. E. White, of San Diego.

Method of Rattle Formation - The Prebutton

Having early been convinced of the accuracy of the theory that a rattlesnake secures a new rattle each time it sheds its skin (although there has not been entire concurrence by herpetologists on this point), I was at a loss to understand why young rattlesnakes, which, like other snakes, shed their skins soon after birth, were not subsequently possessed of two rattles, one to match the original skin with which they were born, and the second, the newly acquired skin. This, however, is easily explained, for it is found that the young rattlesnake does not retain, but, on the contrary, sheds the rattle with which it is born. This birth-rattle will hereafter be referred to as the prebutton. Garman noted the difference in shape between the prebutton (Fig. 48), and the true button or first permanent rattle (Fig. 49), but thought the one was transformed into the other by a stretching, accompanied by a constriction at the outer end and a swelling of the proximal edge, thus acquiring the characteristic shape of the button. This is found to be contrary to what actually occurs; for, from observations of recently born broods, it is found that when the birth-skin is shed the prebutton goes with it. This loss occurs for two reasons; first, the thinness and fragility of the prebutton; and, secondly, because its configuration, and that of the true button beneath, are such that it cannot retain a grip on the latter. The crimped edge of the prebutton is too pliable and weak to prevent opening, and furthermore, the central transverse groove in the button is too shallow, so that there is little for the prebutton to grip. As a result, the prebutton is shed just as the skin itself is lost. Usually it is shed as a part of the skin; in fact, the prebutton is hardly distinguishable from the skin except upon close examination. Its very softness may cause it to be overlooked in the shed skin of the baby rattler.

The fact that baby rattlers shed shortly after birth is verified by observation on broods born in captivity; this is a program characteristic of most snakes, whether oviparous or ovoviviparous. For example, a brood of 14 C. h. horridus were born on September 20, 1934, between 8:30 and 10:30 in the morning. The eyes began to turn blue on September 25th; this cleared up by October first and second. The first snake shed on the night of October 3rd; most of the youngsters shed on the 5th, and all by the 6th. Of a brood of 11 C. ruber born on October 16th, about half shed on October 26th, and the others on the following day. Three, in another brood born August 10th, shed on August 21st. Three C. v. oreganus born August 24, 1937, shed on September 3rd. These observations were made by C. B. Perkins. A. M. Jackley has advised me that he observed that C. v. viridis in South Dakota shed in from seven to ten days after birth; one brood, however, shed in three days. I think that nearly all broods shed between one and two weeks after birth, thereby changing from the prebutton to the button. Barton, 1800, and Curran, 1935, mention juveniles born with two- or three-segmented rattles. Amongst broods totaling several hundred youngsters, I have never witnessed anything of this character. Often the second segment (Fig. 50) is acquired shortly before hibernation, and I have seen broods in which some individuals had attained their second rattles within a month to six weeks after birth. Thus in the San Patricio series of 139 C. cinereous, born in late August and preserved one month later, three specimens had already acquired their second rattles. In the Platteville series of C. v. viridis, collected while entering or leaving hibernation, out of 226 young of the year, 44, or 19.5 per cent, had already achieved a second rattle, and one had three.

Although I think there is only one proper use for the term "button", this being to indicate the first rattle permanently retained after the skin with which it was once coördinated has been shed (Fig. 49), the word has been used in other senses. Hardly a rattler is ever reported in the newspapers unless it is stated to have had "blank rattles and a button". But here button usually means the terminal lobe of the last rattle, even though the string may not be complete, the true button and additional rattles having been lost. Others use the term to indicate the proximal lobe, in the sense that this "buttons" the string to the body. But the term button was originally used, and properly, I think, as the single, soundless rattle of the young rattler (after the prebutton had been shed), which is more button-like than the later segments. As soon as the string is broken, and one or more segments lost, which is quite early in the life of most snakes, the rattler no longer has a button.

The successive rattles are usually of sufficiently different shapes, particularly with respect to the transverse grooves and angularity, so that it is quite easy, after a little experience, to be able to distinguish between the prebutton, the button, and succeeding elements of a string. if, in the latter case, one or two rattles have been lost (Figs. 51 and 52). C. cerastes has a peculiarly shaped button which sometimes makes it rather difficult to ascertain whether it is, or is not, present. The same is also true of C. durissus and its relatives, which have smaller buttons than other rattlers of corresponding size.

Interrelationship of Rattle and Skin; Development of a Rattle Segment

The second divergence from the usual descriptions has to do with the relation between the skin of the rattlesnake and the rattle itself, for these refer to the rattle as a thickened and corrugated terminal section of the skin. It has been stated that when the skin is shed it tears away from this thickened and horny terminus, which is then retained by the corrugations of the succeeding rattle.

While this no doubt explains the genesis of the rattle, the mechanism of formation has become so highly differentiated that its relation to the skin can only be traced with difficulty, and there may be some question as to what element of the skin constitutes the ancestral analogue of the rattle. For, as at present perfected, the rattle is not merely a thickened terminus, but results from a separate and discontinuous deposition. The skin of the rattlesnake actually extends to the tip of the tail, covering not only all exterior portions of the body, but the concealed and corrugated rattle-forming matrix as well. The rattle is formed, not by the thickening of the skin of the matrix, but by the deposition upon its surface, of an entirely separate, clay-like substance, which thereafter hardens and becomes a rattle.

To trace the possible origin of the rattle it will be useful to recall some features of the skin. It will be found that the skin has a duplex character. Those parts which cover scale surfaces are somewhat thickened, and, if shed prematurely, often retain considerable pigment. Surrounding these thicker sections there is a network of thinner elements, which comprise the folds of the skin between the scales--that is, they cover the interstices below the imbrications. As the skin is shed the folds are flattened out; thus the skin takes on a larger area and is easily removed. If a snake be preserved a short time prior to shedding and is subsequently dried, the scale tops will often come off in the form of evenly-edged and separate flakes. But if the skin is naturally shed the scale tops are like clear lenses in the general texture of the continuous skin; they are less pliable than the rest of the skin and are less easily torn. Evidently, in the changes which take place in a skin prior to its being shed, the scale tops are replaced first, and may be separated from the skin, of which they form a part, by the liquid of the preservative before the thinner skin covering the interstices is ready for replacement.

It is believed that the rattle is analogous to a scale top, at least as far as its original derivation is concerned; and just as a scale top seems to be superimposed on a general skin, from which at certain stages it can be separated, so also the rattle is separable from the skin of the matrix upon which it has been deposited. This may be verified by a study of the prebutton, which is intermediate in character between the body skin and the perfected rattle.

The development of the rattle can be best described by assuming that we are watching the formation of a new segment, as it would be seen if we removed the previously formed segment; for the latter ordinarily conceals, as a protective roof, the posterior corrugations of the matrix upon which the new rattle is to be formed. We shall consider in this outline a typical adult rattle having three lobes. The last two would be disclosed by the removal of the prior rattle; the anterior of the three will be formed under the tail skin which is next to be shed.

We picture, then, the rattle-forming matrix with its three transverse corrugations. It is covered with a thin skin, which is apparently a continuation of the skin which will be the snake's exterior covering after the next shedding. Upon the surface of this skin the rattle is now deposited, in the form of a laminated grayish, opaque, and clay-like material, presumably extruded from glands within the matrix. This material remains soft, and, if picked off with a sharp instrument, comes away from the skin in irregular flakes. The laminations are easily seen and the separation from the skin below is quite clear. The anterior or proximal edge of the solidifying rattle is entirely definite and even; there is no confusion with, or adhesion to, the new skin, such as would be expected if the rattle were simply a thickened patch of skin.

The grooves in the matrix are not rounded in outline; rather, the corrugations have a shrunken and angular appearance; to these the soft and newly formed rattle closely adheres.

When the deposition of the rattle has been completed, the material hardens. It becomes thinner, denser, and quite transparent. The skin below acts as a parting strip, or separating surface; and when the hardening is complete, the rattle springs away from the deeply indented and angular matrix beneath, and assumes the more rounded outlines which characterize the finished rattle. There is evidence that the hardening progresses by laminations; at least, specimens are found with a transparent surface layer like cellophane, while below there still remains a thin sheet of the amorphous clay-like material.

The shape of the new rattle is determined by the matrix, not by the posterior or older rattle acting as a mold, as some authors have suggested. Such would be impossible, for no mold would be available for the anterior lobe. There is always considerable clearance between a newly formed rattle and its predecessor, until the newcomer springs away from the matrix upon completion.

When the proper time arrives and the new rattle is completely hardened and finished, the old skin is shed, thus uncovering for the first time the anterior lobe of the new rattle segment. The two posterior corrugations are, of course, covered by the anterior and middle corrugations of the previous rattle, and thus they are not disclosed. (This is the normal condition; in our description we had assumed the previous rattle removed, so that the formation of the new segment might be observed.)

One point in this process remains to be described, namely, the relation of the new skin, which now constitutes the exterior covering of the snake, and the new rattle. As previously stated, this skin is not attached to the new rattle. On the contrary, it is first lapped, in a deep fold, over the outside of the anterior edge, or bead, of the rattle, and thence passes underneath, where it is apparently continuous over the matrix, in the form of a soft white exudation, which is probably the analogue of the skin in the interstices between scale tops. Sometime during the life of the new rattle this soft material must dry out and disappear, either as broken flakes or otherwise. It cannot be reabsorbed into the matrix since it is found that the next rattle has begun to form before it has disappeared. This soft material is not only a possible analogue of the skin, but it is also related to the transfer of the lobes of the matrix, subsequently to be described.

The prebutton suggests a transition stage between the ancestral skin and the final rattle mechanism, thus serving to indicate the analogous elements. Here the true rattle is so thin, compared with the skin itself, that it is carried away with the skin; it is found to be but a thin, transparent capsule over the skin. However, while the skin is continuous over the body and to the tip of the tail, the prebutton covers only the rattle portion. Thus the prebutton seems to be an intermediate stage between the transparent skin, which covers the scale tops, and the rattle; the skin below, from which the prebutton may be readily separated, corresponds to the lower layer of skin over the body, of which it is seen to be a continuation. No doubt in the prebutton we have a glimpse of an earlier stage in the evolution of the rattle. Also, we have a proof that the skin changes on the matrix just as it does over the rest of the body surface.

The fold of the skin over the bead, or outwardly curved, anterior edge of the rattle, is important, since by stretching, as the rattle slips back, it makes available the additional space under which the anterior lobe of the next succeeding rattle is produced. In any snake (not a rattler), just prior to shedding its skin, each scale and fold of the old skin exactly corresponds to the same scale and fold of the new skin below. This is not true of the tail of the rattlesnake. Just anterior to the rattle, for a short time before a skin is shed, the completion of the proximal lobe of the new rattle and the slipping back of the old, causes the old skin to loosen and stretch, and become the protective covering of the growing lobe of the new rattle. This stretching is permitted by the fold over the bead previously mentioned; and after the stretching has taken place, it will naturally be found that, toward the end of the tail, the scales of the old skin do not correspond in position with the scales of the new skin, but have been longitudinally displaced, relative thereto, for as much as a centimeter or more in the larger snakes. During the stretching process the end of the old skin is held in place by being caught in the folded edge of the rattle which is slipping back.

Coincidence of Shedding with Rattle Formation

While most observers have agreed that the formation, or at least the disclosure of each new rattle, is coördinated with each change of skin, there have been some dissenters, notably Hopley, 1882, and Feoktistow, 1889 (translation, 1891). Others have doubts, as for instance, Storer and Wilson, 1932. Curran and Kauffeld, 1937, express the opinion, said to be verified by laboratory observation, that, while no new segment is added without the shedding of the skin, the skin may be shed without producing a new rattle. But it seems to me evident that these conflicting observations were largely made on captive or defective specimens;* and I have already pointed out how seriously the natural processes of these reptiles are interfered with by the artificial conditions of captivity, if they are not given great care, or if they refuse to eat naturally. Here we see them sluggish, a prey to starvation and disease, their skins shed at irregular intervals, and often in strings and patches rather than entire as in a healthy snake. Small wonder then, that the observer is unable to note whether a fresh rattle is disclosed coincident with each shedding, or whether the total rings acquired in a given period equal the number of moults in the same time. Even where the skin is shed entire, the posterior end may pull away from the previous rattle and disclose the new segment several days or weeks before it is shed. Under such circumstances, unless the rattles are carefully counted, an addition will not be noted as accompanying the skin change. Also, it is possible that a segment may be lost at about the time the new rattle is disclosed, and this would not be observed unless each segment were marked or numbered.

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* Hopley's was obviously a deformed freak.

Those who have postulated an independence of shedding and rattle acquisitions, have failed to note the continuity of the skin, over the visible part of the body, with that covering the hidden matrix. The anterior ring of the nascent segment is always developed under the protection of the posterior end of the visible skin. Were the two unrelated chronologically, the new rattle would either have to be developed in the open (which would give it no protection in the lamellate stage), or the skin of the tail would have to break away from the crimped selvage of the old rattle and regrip the new. That the dead skin can do this is obviously impossible. It would seem equally impossible for a new skin to be formed over the crimped selvage of an old rattle.

But in healthy snakes we know from a study of large numbers of specimens in all stages of the process, that the shedding of each skin uncovers the anterior lobe of a new rattle; the fact that each skin really extends to the tip of the tail and, therefore, every pair of rattles is separated by a skin, allows of no other interpretation than that each exuviation means a new rattle.

As examples of the distortion of the life cycle which sometimes occurs in captivity, I might mention a *C. v. oreganus* which was kept alive some three years. At the end of that time it had a complete string of ten rattles, but the length of the snake was only about 60 per cent of normal. Another even more striking instance, in which prenatal influences may also have been effective, is presented by a *C. v. viridis*, born to a captive specimen September 24, 1932. This young rattler died a year later on October 2, 1933. At that time it was possessed of an unbroken string of nine rattles where, had it led a normal existence, it would have had five, thus showing the effect of the avoidance of a winter hibernation. But, far from profiting by this increased activity, at death it had a length only half that of a normal snake and the final rattle had but 56 per cent of the width of a normal ninth ring.

Mrs. Grace Olive Wiley was kind enough to show me one of her remarkable captive-bred litters of rattlers. This was a brood of 9 *C. cinereous*, born June 17, 1932; I saw them on September 20, 1934. Four of these had complete rattle strings, 3 with 15, and one with 14 segments; one had lost only the button and had 15 rattles left. The others had broken strings. The remarkable features of this group are the high number of rattles at the age of 27 months, no doubt due to forced feeding and the absence of hibernation; and the large proportion of complete or almost complete strings, resulting from the snakes being undisturbed. But the rattles were not normally proportioned for *cinereous*, being smaller than the usual size, showing either a more frequent ecdysis than usual, or a less rapid body growth. As 14 to 16 rattles at the age of 27 months is no doubt greater than normal, probably both causes distorted the rattle strings. Of course, these are extreme instances of the irregularity of growth due to captivity; other cases are cited in the literature, of specimens bred, born, and grown in captivity, which more nearly approach the normal. C. B. Perkins raised three captive-bred *C. ruber* which were born on August 10, 1937. On February 17, 1940 (age 30 months) two had complete strings; one 9, and the other 10. These are well within the limits of the number of segments that wild rattlers of the same age would ordinarily have. Also, it may be noted that a record was kept of the shedding of these snakes; the number was found to correspond to the number of rattles. However, it is only too evident that the life cycle cannot be judged with assurance from a study of captive specimens.

Whether the rattle continuously increases in size during the life of a snake, is closely involved with the question whether adult snakes grow slowly, but continuously, until their deaths, instead of reaching a definite growth-limit rather early in life, as do mammals and birds. This has been discussed in Part IV of this series (Occ. Pap. No. 3, p. 31, 1937) and will be mentioned again in the study of rattle dimensions. Since the rattle size is determined by the dimensions of the matrix, there is a high correlation between body size and rattle size during the early period of rapid growth; this correlation is less evident in the time of slower growth during the adult stage, since the size of the matrix is affected by body nourishment more than by body growth. Hence there is occasionally evident a cyclic variation in size, correlated with seasonal activity and the availability of food. And under extreme conditions, such as the effects of brush fires on food supply, or self starvation in captivity, there may be a marked diminution in rattle size as new segments are added. Later, with a recurrence of normal conditions of nourishment, the dimensions may again return to normal.

The early pictures of rattles showed a continuous growth and steady increment in the size of the successive segments (Fig. 53). Such pictures of unbroken strings of 32 and 37 rattles will be found in Seba, 1734, plate 95; and Shaw, 1802, plate 91, shows one of 44 segments. As a matter of fact, the growth is rapid up to and including rattle No. 6, and then continues at a reduced rate up to rattle No. 12, or 14 (Fig. 54), declining more rapidly in females than males. Beyond this it is impossible to tell whether there are any further increments, for, if present, they are so small as to be completely masked by seasonal and other variations, as previously mentioned. At any rate, beyond rattle No. 12, the rings are of substantially equal size, and the sides of the string are parallel. There are certain indications that shedding (and therefore the acquisition of new rattles) is less frequent after full adult size is attained; however, this is a matter requiring further study.

The Rattle-Shifting Mechanism

We now come to the third element in the rattle formation, which, it seems to me, has not been adequately explained. It has been merely stated that when the time comes for the formation of the new rattle, the old segment slips back one corrugation, thus leaving the new segment a corrugation in advance. This, however, is a mechanical operation of considerable intricacy requiring further explanation. It must be remembered that, after the completion of an adult rattle, we have a rather rigid object having three lobes, or corrugations, which surround three similar lobes of the rattle-forming matrix below. There is not close adherence here, for, as has been stated, the rattle has sprung away from the matrix in the drying or setting process. Nevertheless the lobes of the matrix are sufficiently large so that they cannot slip forward through the constrictions which constitute the transverse grooves of the rattle. We have, then, the problem of effecting a relative longitudinal displacement of one lobe between the matrix and the rattle; that is to say, either the rattle must slip back one lobe, or, what constitutes the same thing, the matrix must travel forward one lobe, so that its middle lobe will engage the anterior lobe of the rattle.

This might be effected in several ways. For example, the lobes of the matrix might be decreased in size, until each would pass through the constriction of the rattle immediately in advance of it. However, if this were done, it is evident that the rattle would no longer be held to the tail; it would slip off the now-tapering matrix and be lost.

It might be possible that, as the matrix becomes tapered, as above suggested, the skin would grip the bead of the rattle, and, by stretching, permit the rattle to drop back one groove, although preventing a backward passage beyond this point. But, this leaves much to be desired as a safe mechanism, since a tearing of the relatively fragile skin during the process would cause the loss of the latest and all prior rattles. This would frequently result in a situation seldom met in nature; for although snakes often have incomplete strings, they are rarely found with a single rattle, such as would be the case if they were collected immediately following an accident such as has been described.

It seems to me that the only satisfactory explanation of the relative movement between rattle and matrix, which will comply with the mechanical necessities of the case, is to visualize a sort of wave action in the corrugations of the material constituting the tissue of the lobes, relative to the surface skin and the bones beneath. One might observe this effect by picturing two tight rings on the finger of a glove. The rings are the rattle constrictions; the bulges between are the lobes. Assume some internal force to cause the bulges to move toward the end of the finger. The rings will be carried along, slipping over the glove surface (the skin) and always separated by, and held in place by, the bulges. In the same way, the matrix skin formerly covering the anterior lobe moves forward, relative to the rattle, until it occupies the location where the anterior lobe of the next rattle will subsequently appear; and a swelling begins at this point which constitutes the reappearance of the anterior section of the matrix in its new position. Yet this has been effected while still maintaining a lobe of the matrix continuously within the anterior lobe of the displaced rattle. So it is that the second matrix lobe, now somewhat decreased in size by the exudation of some of its substance in the form of a white, jelly-like material, occupies a position below the anterior lobe of the elder rattle. Similarly the terminal or third lobe of the matrix is now below the middle corrugation; and the original final lobe is now represented only by the soft white jelly; it is without structure, for bones and skin have moved forward. Hence the matrix is in position for the formation of the new rattle, which will be properly interlocked with the old. This process is aided by the clearance between the matrix and the rattle, the latter in the hardening process having sprung away, as previously mentioned.

The query may be made as to the necessity for so involved a description of so simple a process, for the old rattle has merely slipped back one lobe. The point is, that during this process, it is necessary continually to maintain, under each rattle lobe except the last, a lobe of the rattle-forming matrix, for otherwise the rattle would be lost in the transfer; and the only means whereby this can be effected is by the relative surface movement of the skin, coördinated with a wave movement and exudation of the matrix tissue as above described.

The process will be more clearly understood by reference to Figs. 55 to 58, inclusive, showing several transition stages; this is a schematic, rather than an accurate dimensional presentation. Attention is particularly directed to the movement of P, a single element of the matrix surface; especially is it to be noted that the motion of P is wavelike, for it occupies at various times both the bottom of a corrugation and top of a lobe. Note also how the point P' on the rattle, originally opposite P on the skin, gradually drifts away from it. And finally the reader may concentrate his vision on the vertically cross-hatched matrix in the four figures in quick succession, and see how it seems to crawl forward, while always retaining a bulge behind P', thus preventing the escape of the old rattle, until the new one has been formed below.

By observing a large number of rattlers, especially some just before, during and after exuviation, we should find all stages in this scheme of transfer, thus verifying the method by a serial picture of the process. This has been done by baring the matrix on a large number of snakes; the surface, or completed rattles, were removed to disclose the conditions below, both in the matrix and the incomplete rattle in process of formation, and specimens were found representing all stages in the longitudinal method of transfer above outlined.

Probably the most striking illustration of the transition is to be seen in the change which takes place in the third, or posterior lobe, of the rattle about to be slipped back. For here we have the tip of the matrix and the end of the rattle itself, and, therefore, two points of reference whose relative positions may be easily noted.

First we find the matrix completely filling this terminal lobe; the rattle, newly formed, clings closely to it, following each sharp angle. Next we find that the rattle has sprung away from the matrix. Then the lobe of the matrix seems to shrink; a space is seen between it and the rattle, which fills with a soft, white substance of the consistency of jelly. This movement continues; the lobe of the matrix diminishes in size, the tip of the tail moves forward relative to the end of the rattle, and the space thus vacated is filled with the amorphous jelly. Finally the posterior point of the matrix has advanced through the constriction between the third and second lobes of the rattle until it comes to rest in the second lobe; and the posterior lobe is vacated save for the jelly.

While this change has taken place in the third lobe, a similar transformation is effected in the first and second bulges, but here the change is not so evident. We note only that the lobes on the matrix decrease in size and move backwards, relative to the skin which covers them and the vertebrae which constitute their core. As they shrink, the space vacated partly fills with the jelly; it is particularly evident on their posterior shoulders, but does not

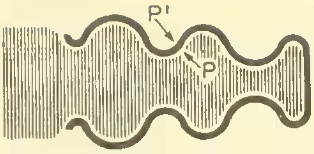

Fig. 55

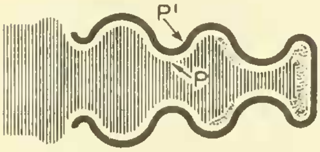

Fig. 56

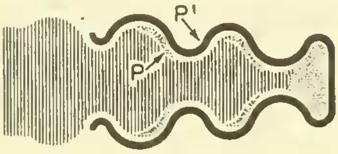

Fig. 57

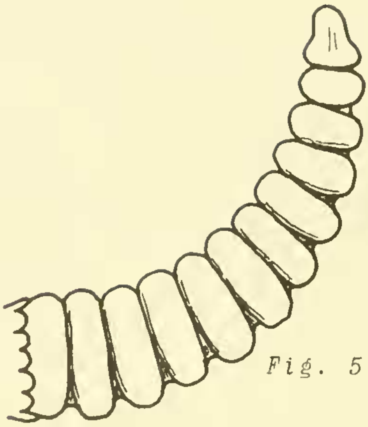

Fig. 59

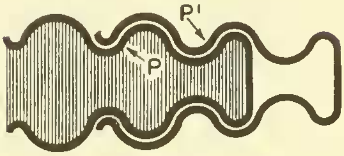

Fig. 58

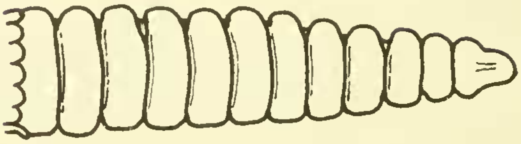

Fig. 60

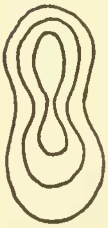

Fig. 61

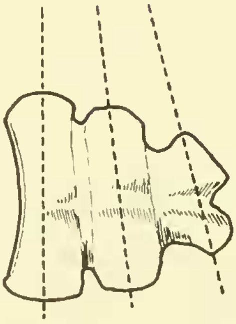

Fig. 62

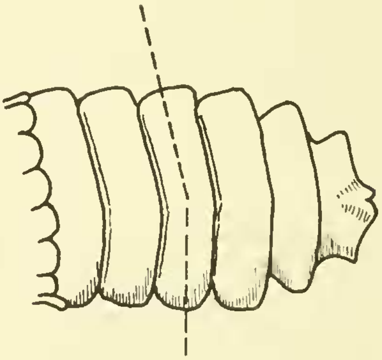

Fig. 63

Fig.55. Schematic diagram of rattle transferrence.
" 56. (P is a point on the surface of the matrix
" 57. and P' a point on the rattle. The dotted
" 58. material is soft and amorphous).
" 59. Rattle string with the outer end raised to its highest position, showing the effect of the asymmetry on the possible travel
" 60. The same rattle string as in Fig.59 with the outer end in its lowest position
" 61. Vertical section showing the asymmetry of the internal fit of three interlocking segments
" 62. Lateral asymmetry of a rattle segment
" 63. Forward slope of the upper lobe

completely fill the space between rattle and matrix, tending to adhere to the former. The longitudinal movement is now complete; the new rattle can be deposited on the matrix in its new position; and the jelly, evidently the analogue of the skin which is about to be shed over the rest of the body, disappears, probably by dessication. (It was found by experiment that the jelly, if left in the air, quickly dried to a colorless film not greatly different from shed skin. Its condition, as examined, may be somewhat affected by the preservative.)

We judge, from the comparative prevalence of specimens in these several stages, that the presence of a complete rattle over the matrix is a relatively stable condition, while the slipping back followed by the deposition of the new rattle is a transitional situation occupying a shorter period of time. No doubt this phase of the process corresponds to the relatively short period during which the eye of a snake is dulled by an incipient exuviation.

We may state, in further verification of the mechanics of transfer thus outlined, that the length of tail of the rattlesnake is virtually unchanged in this intermittent process; that is, the anterior edge of the rattle-forming matrix (not the anterior edge of the last visible rattle) is always at the same distance from the anus. The number of subcaudals and the dorsal scales on the tail remains unchanged.

We know, also, that the corresponding lobes of successive rattles are always cast upon the same area of the skin covering the matrix, for, if this be damaged, thereby causing a defect in the rattle, the same defect will reappear at a corresponding point of the equivalent lobe in each succeeding rattle segment. For example, in a specimen of C. ruber having a complete string of eleven rattles, there was, on each anterior lobe beginning with the fifth, a pair of longitudinal striations. These were found on no other lobe of any segment. On the surface of the matrix itself there was a sharp ridge corresponding to these striations and duplicated nowhere else on the surface; this, obviously, is the surface indication of the damage to the rattle-forming mechanism which must have been sustained at the time the fifth rattle was being formed, and which, ever since, has had its effect on each succeeding rattle.

In another instance a specimen of C. cinereous had a scaly imbrication, or flap, over a corner of each anterior lobe; this was found to be due to a similar flap of skin-covered tissue over the corresponding lobe of the matrix. similar defects are comparatively easy to find in large series of rattlers and always they are repeated at the same point of each succeeding rattle.

Structure of the Rattle

The rattle is too irregular an object to permit a universally satisfactory description; however, certain generalizations may be made. It is known, of course, that, as the rattle is carried by the snake, the greater dimension of each ring is vertical and the lesser transverse; that is, the rattle is carried with the broader, flatter sides as lateral faces.* In addition to the deep transverse grooves, or constrictions, which separate the lobes of each rattle, there is a secondary longitudinal furrow, sometimes narrow and sharply indented, more often broad and shallow, along the lateral faces of the exterior lobes. The longitudinal groove of each superior lobe loosely engages the groove in the inferior lobe beneath; thus it affords a certain stability, by guiding movement, and, by its corrugation, increases strength. In the hidden lobes, the longitudinal grooves are deep and sharply angular, so that the engagement of the groove of the second lobe with that of the third is quite restrictive. Often these internal furrows are so deep and compressed as to produce internal reinforcing fins.

The device which permits the snake to carry his rattles clear of the ground is the result of an asymmetrical development above and below the longitudinal furrow. Necessarily there is a looseness of fit, or lost motion, in the coupling of the successive segments; this is required for the use of the rattle as a sound producer. Were it constructed symmetrically about the longitudinal center line, this looseness would result in a downward curve, which would allow the posterior rattles to drag. But the rattles are not symmetrical; on the contrary, each ring is so distorted that, when the rattle string is in a position permitting equal degrees of freedom both upward and downward, the center line is a curve upbending posteriorly (Figs. 59 and 60). When the limit of travel downward, as permitted by the successive interlocks, is effected by the weight of the rattle, the center line is virtually straight. By this means a slight upward tilt of the tail end suffices to keep the rattle clear of the ground and this is the snake's normal crawling posture.

The method whereby the asymmetry is produced is ingenious. Each flat side of a rattle is grooved by the central longitudinal furrow. This is rounded, and may be wide or narrow in the anterior surface lobe, but in the concealed lobes it is deep and sharply cut. This furrow serves both as a reinforcement of what would otherwise be a weak, flat surface, and as an interlocking guide between the meshing lobes. Thus each lobe is virtually divided into two halves; looked at endwise the halves appear like intersecting cylinders. So deeply cut by the side grooves is the innermost lobe, that, from the end, the two cylinders seem connected only by a thin vertical web. The important point with reference to the asymmetry is that the upper half of each exterior lobe is smaller than the lower half, while the upper halves of the interior lobes are larger than their lower counterparts. Thus the fit in the upper half between the exterior and interior lobes is closer than in the lower halves, and the limit of travel in any direction is first reached in the upper half (Fig. 61). This is further accentuated by a longitudinal compression of the transverse grooves and lobes in the upper half as compared with the lower; each separate rattle is therefore curved slightly upward as if it were a segment of a circle of large diameter (Fig. 62). In large specimens a third, but related, type of asymmetry is clearly evident; this is a forward slope of the

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* Rather surprisingly this was once the subject of controversy in the correspondence columns of a magazine devoted to hunting and fishing

upper lobe, which is at an angle with the lower (Fig. 63).

The effect of the asymmetry can best be visualized by the following simple experiment: First, hold a long rattle string in the position as it is carried by the snake and it will be observed that it is straight. Now turn it upside down and the whole structure sags; if the string be long enough, the last links will hang vertically downward. Another method of showing that the mid-position of a rattle string is a curve, is to press the two ends of a long string toward each other so as to reduce the lost motion to a minimum. It will be found that the string assumes a curve, with the end tilted upward.

Not only is this asymmetry important in procuring a safe carrying position, but, also, it has a beneficial effect in sounding the rattle. When the rattle is to be vibrated, the maximum effect will be produced, with the least wear and consumption of energy, if the several clashing elements are balanced on their center lines. Were the rattle symmetrical, the tail would have to be vertical to secure this balance, and the rattles would tend to fall in a curve either forward or toward the rear. But with the difference in weight and size between the halves, an angle of some eighty degrees with the horizontal will suffice to hold the rattles in a straight line, and this is the angle at which the rattler in the striking coil usually sounds his rattle. Occasionally, however, it will be held farther from the vertical, but still the asymmetry keeps the string straight instead of drooping.

The articulation of the rattle is necessarily loose, yet it is surprising how difficult it is to remove successive rings, particularly adult segments with a full complement of transverse grooves, so effective is the clinch or interlock. The fracture and complete removal of an exterior lobe at the center of a string will not cause the loss of the rattles posterior thereto, as they are still coupled by the smaller and stronger lobes within. So rattles, unless cut or broken clear through, must be worn off and lost in succession from the posterior end forward, and each lobe of a segment must be completely fractured before detachment finally occurs. Hence we see how these relatively fragile members are so tenaciously retained.

As an indication of the looseness of the articulation it may be noted that a string of adult <u>oreganus</u> rattles 12 mm. in width and 42 mm. in length when adpressed, measured 48 mm. when fully extended, thus showing a longitudinal lost motion of 6 mm. per ring, or 13.3 per cent of the normal string length of 45 mm. A string of 12 <u>adamanteus</u> rattles 78 mm. long had a lost motion of 12.8 per cent; and a set of 15 <u>tortugensis</u> rattles 86 mm. long, 8.3 per cent. All of these strings were fully adult, that is, the posterior rattles were of substantially the same size as the proximal.

In all rattles the interior lobes are more sharply angular than the larger, outer lobe. I have hitherto mentioned the bead, or narrow outward curl, along the lateral anterior edge of each rattle. Usually this bead is doubled back and flattened against the rattle to form a sort of hem or selvage, a device beautifully designed to prevent the start of a tear. Also, in the striking of this folded edge with the shoulder of the next anterior rattle, we have one

Fig. 64

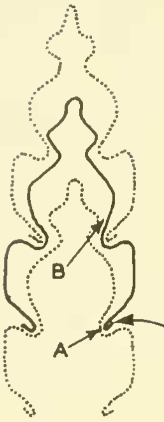


Fig. 65

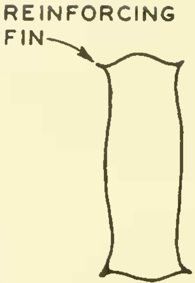


Fig. 66

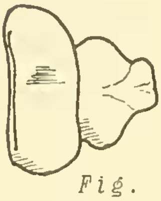


Fig. 70

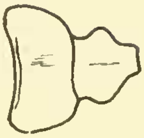


Fig. 69

Fig. 68

Fig. 67

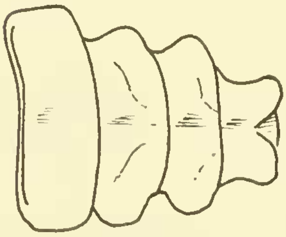


Fig. 73

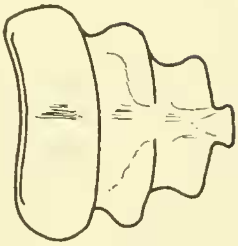


Fig. 72

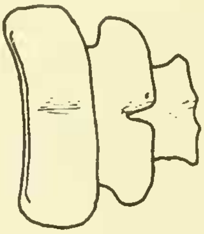


Fig. 71

EXAMPLE RATTLE SEGMENTS; UNBROKEN STRING FROM C.cinereous.

Fig.64. Vertical cross section of interlocking rattles (Two are dotted to facilitate identification).

" 65. Horizontal cross section of interlocking rattles (Through the center of the lower lobe).

" 66. Vertical cross section at the bottom of the anterior groove, showing the reinforcing fins

" 67. Prebutton

" 68. Button

" 69. No.2 rattle

" 70. No.3 rattle

" 71. No.6 rattle

" 72. No.10 rattle

" 73. A four-lobe segment

of the contacts producing the noise, the bead being a reinforced wearing surface (point A, Fig. 65). The other principal point of contact is between the heavily stiffened posterior lobe and the transverse groove of the outer rattle (point B). These contact points produce the maximum noise with the least friction and wear.

Another ingenious development is the reinforcement of the transverse grooves between lobes by tiny ribs at the four corners, for these grooves, as viewed in section, approach a rectangular, rather than elliptical, shape. Between these ribs, at top and bottom, the interlocking clasp of the first lobe is particularly effective, the grip being almost claw-like; at the same time it acts as a hinge, permitting unimpeded side movement in the direction taken by the vibrating rattle (Figs. 64 to 66, inclusive).

An outline of the changes in size and shape, in the successive segments of a string, can best be exemplified by a description of the elements of a typical unbroken string. A ten-rattle _C. cinereous_ was selected for this study.

_No. A_ (Prebutton, Fig. 67). (This is a hypothetical description of this unit, since it disappeared with the first shedding after birth. It is described from specimens of recently born young.) This is flat and single-lobed. The vertical cross-section is elliptical. The central longitudinal furrow is evident but not deeply indented. The material is thin, flexible, and transparent, and the entire rattle rather easily removable because it is only slightly constricted at the clinching end. It does not tear easily. From a side view, the posterior end is semicircular in outline. The thickness of material is about 0.015 mm.

_No. 1_ (Button, Fig. 68). There are two lobes only, and these not sharply differentiated; both are smooth and rounded in outline. The anterior constriction is adequate for holding and a slight bead is evident on the edge. The groove between lobes, while distinct, is shallow, particularly on the sides, and not clearly defined. The longitudinal furrow is continuous from end to end and is deeper posteriorly, thus pinching the end into upper and lower sections. A vertical asymmetry is already in evidence, the transverse groove being deepest above.

_No. 2_ (Fig. 69). Of this rattle the second (or posterior) lobe is completely developed and the first transverse groove sharply cut. The third lobe is in evidence, but has no holding power. The bead on the first, or anterior lobe, has become folded into a hem.

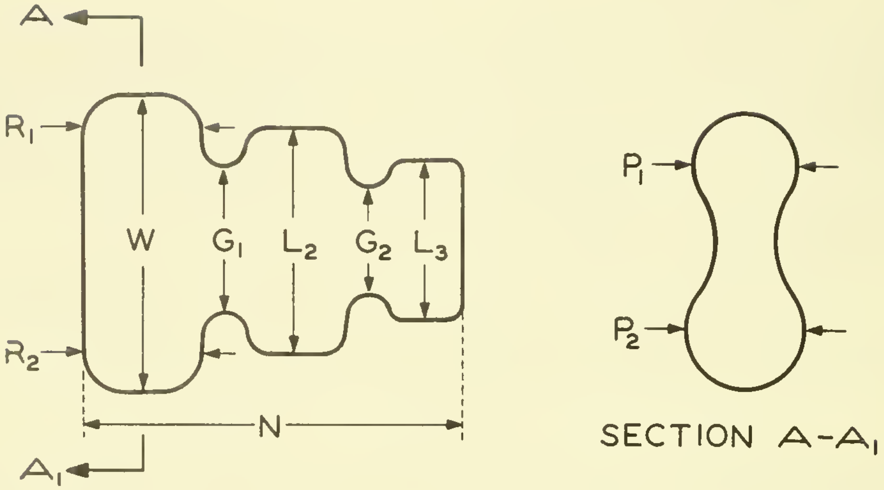
_No. 3_ (Fig. 70). There is little change from the previous rattle except that the third lobe is better developed; it takes the form of two parallel horizontal cylinders connected by a web. The vertical asymmetry is more in evidence.

_No. 4_. Of this rattle, the posterior (or third), lobe is considerably enlarged by the outward divergence of the two cylinders; it now has considerable holding power, which is of importance in retaining rattle No. 3. The reinforcing ribs at the corners of the transverse grooves are clearly in evidence, but more so in the anterior groove between the first and second lobes. Viewed from the interior, these ribs are seen to be of importance in strengthening the

Table 33

DIMENSIONS OF A RATTLE-STRING

C. cinereous



Rattle Number	W	L_2	L_3	G_1	G_2	N	R_1	R_2	P_1	P_2	Wall Thickness
1	64	51	-	47	-	82	29	31	40	45	0.23
2	75	50	29	39	27	87	38	34	46	53	0.25
3	88	63	31	44	25	97	43	40	56	60	0.28
4	103	75	39	55	31	113	45	44	60	68	0.31
5	117	90	54	66	41	117	48	43	69	75	0.36
6	127	100	63	73	49	123	50	46	73	81	0.43
7	133	106	73	77	56	122	48	43	76	84	0.36
8	139	116	78	85	60	120	49	44	75	83	0.43
9	144	123	88	88	69	133	50	46	78	85	0.46
10	156	126	93	94	71	146	55	50	82	92	0.51

All dimensions in mm./10

structure. The clinch of the first lobe is particularly effective at the vertical ends, that is, at top and bottom, comprising a veritable claw, which grips the groove between the corner reinforcements of the second lobe of the No. 5 rattle.

No. 5. The third lobe is now structurally of considerable importance. Viewed from the posterior, so that each lobe appears as a small circle, concentric with its larger anterior fellow, it can be seen that the anterior or outer lobe has a larger lower than upper segment, while the contrary is true in lobes two and three.

No. 6 (Fig. 71). The third lobe is still further enlarged. The posterior surface of the middle lobe is deeply indented.

No. 7. The transverse grooves are still deeper and more sharply indented.

No. 8. There is little change beyond an enlargement of the parts.

No. 9. Now for the first time the divergent cylinders which constitute the posterior lobe are extended into little cones as if a fourth lobe were in contemplation. The transverse grooves are deep set and angular, and the asymmetry more than ever evident.

No. 10 (Fig. 72). This rattle, the proximal or attached rattle of the present string, surrounds the matrix from which it has only partly sprung away. The tentative conical extensions from the rear of the posterior lobe have become more prominent.

Dimensional data on this typical string are set forth in Table 33.

Whether, had this string grown further, a complete fourth lobe would have been developed, is not known. Four full lobes are occasionally found (Fig. 73), particularly in the larger species, and sometimes the beginning of a fifth has been observed. I have been unable to determine whether the development of a fourth lobe is characteristic of a particular age, sex, or species--the indications are rather against consistency on this point. I have seen some long strings of twelve or more rattles in which the eldest showed by its form that it was an adult ring, thus indicating that the youngest was at least rattle No. 20, yet no fourth lobe had begun to form. So it appears that three-lobe segments are typical of most adult rattles. The second lobe is evident, but not serviceable, in the button; it becomes effective in rattle No. 2. The third lobe normally is evident in rattle No. 2, and first becomes truly effective in rattle No. 4. By the time rattle No. 7 is attained, the adult shape is reached. Thereafter the increase in the size of successive segments is much slower; this increase continues at least until the twelfth or fourteenth rattle, and possibly beyond; however, after the twelfth it is so small as to be masked by seasonal fluctuations.

Species Differences

The intraspecific dimensional irregularity of the rattle generally inhibits its use as a key character, except where the differences are considerable; for example, that between *S. miliarius* and *S. catenatus*. However, there are definite specific and subspecific differences, not only in rattle size proportional to body size, but also in the growth equation. Data on this phase of the rattle are quite extensive and will be the subject of a subsequent report.

While specific differences in form and color are obvious, they are not sufficiently striking or constant to be always in evidence. It is, in fact, surprising to note the morphological similarity of the rattle, in forms so widely different in other characteristics as are some of the rattlesnake species. The general scheme of the interlock, the support effected by vertical asymmetry, the longitudinal side furrows, the bead or selvage, the fin-type reinforcements of the grooves--all of these intricate perfections are found in every species. The two incomplete lobes of the juvenile button are, in all forms, succeeded by the three fully interlocked lobes of the adult.

There are differences in the angularity and radii of the curves of the lobes, the rattles of some species having a more rounded appearance than others. This is particularly characteristic of *Sistrurus* and the smaller species of *Crotalus*, such as *triseriatus*, *willardi*, *lepidus*, *cerastes*, and *polystictus*. Of the larger species having this rounded form, *horridus* is the most outstanding.

Some of the smaller snakes, especially *polystictus*, *cerastes*, and *triseriatus*, have smaller transverse dimensions proportionate to the vertical (the ratio P_2/W in Table 33) than other snakes; also some, particularly *cerastes* and *triseriatus*, are compressed longitudinally, i.e., the ratio N/W is reduced.

When a rattle still surrounds the forming matrix, it is practically transparent and therefore seems to have the color of the skin below. However, when it has been cast off it loses its transparency (although remaining translucent) and through oxidation, or surface wear, assumes, in most species, a characteristic straw color. Some, however, take on a darker brown hue; this is particularly noticeable in *adamanteus*, *horridus*, *polystictus*, *lepidus*, *tigris*, *willardi*, and all species of *Sistrurus*.

The color of the matrix (in reality a part of the body pattern of the snake) is quite consistent and distinctive. Usually it assumes the color of the final tail ring. Thus, in the members of the *cinereous* and *viridis* groups, and in such forms as *horridus*, *polystictus*, *molossus*, and *durissus*, it is usually black, especially anteriorly. Some forms are partly colored; *scutulatus* is almost invariably black dorsally and light below, while *cerastes* has a black anterior lobe and light posterior. *Sistrurus* and *enyo* are likely to be mottled. *Lepidus*, *triseriatus* (including *pricei*), and *willardi* are pink, the latter with distinct black dots on the matrix. *Tigris* has a grayish or pinkish matrix; this character is so consistent as to constitute a key character, in comparing with the subspecies of *mitchellii*, which have black matrices.

Once having been slipped back, so that the matrix is no longer visible within, it will be found that the color of the rattle is entirely independent of the matrix upon which it was originally formed; thus _ruber_ rattles, formed on a black matrix, are light, while _tigris_ rattles are dark, although the matrix is light gray or pink.

In discussing rattle and matrix colors, it should be understood that only normal processes are considered. If a skin about to be shed, be removed before its time, as frequently happens in the course of preservation, the uncovered rattle (or the matrix below) appears gray-blue in color; this is the effect of the clay-like deposit which has not yet been transformed into the transparent rattle substance, and is entirely independent of the true matrix color. It is an artificial condition and should be neglected in judging the true color of the matrix.

Use of the Rattle by Man

The rattle has not proved particularly useful to man. It has occasionally been used as a decoration, especially with snakeskin belts and hat bands. There is some sale for rattles in curio stores. Mr. C. B. Perkins tells me they are placed in guitars in Mexico to make a sound accompanying that of the strings.

Most people, having killed a snake, carry the rattles home as trophies. There have been accidents when the rattles have been cut from the tail of a supposedly dead snake.

Certain Indians are said to have held the belief that the number of rattles on a snake indicated the number of his victims. Other tribes used the rattle for medicinal purposes.* Some ancient stone carvings incorporated the rattle as a decorative motif.

Acknowledgments

I wish to voice my appreciation of many pertinent suggestions from Mr. C. B. Perkins, and editorial supervision by Mr. C. G. Abbott. Figures 48-50 and 55-58 were prepared by Mr. L. C. Kobler, and 51-52 by Mr. Norman C. Bilderback.

Summary and Conclusions

1. The many purposes attributed to the rattle in the past are listed, including the warning signal, mating call, call for assistance, and lure for prey. That the rattle is used as a warning cannot be questioned, as such use is the normal and almost universal rattlesnake reaction observed in the field. However, it is essential to differentiate between three types of warning: the warning of intruders, possibly dangerous to the snake; an altruistic warning, solely for the protection of the intruder; and the warning of prey. A confusion of these has led to doubts respecting the warning theory; when confined to the first--the warning of possibly injurious enemies--it is logical and in conformity with field experience. The warning is effective in repelling enemies or unconscious intruders, both because of the

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* Long's Expedition to the Rockies, Vol. 1, p. 236, 1823

stridency of the rattle and the other threatening actions of the snake. The argument, sometimes used, that the rattle as a warning is disadvantageous to the snake, by calling it to the attention of enemies is not important. The rattle does not sound unless the snake wills it; dependence is placed on procrypsis, and the rattle is not used until this fails. While probably disadvantageous in the case of man, this is not a valid argument against the warning theory, since the rattle was developed long before the appearance of man in the western hemisphere.

2. A specialization of the warning theory favored by many herpetologists assumes the ancestral rattle to have been developed as a protection against being tramped on by large ungulates similar to the bison. Many genera of snakes vibrate their tails in anger or as a threat. This habit, together with a gradual modification of the normal ophidian tail-spine to conserve successive sheddings, would increase the noise and aid in protecting the owner; for the bison, injured but not killed by a bite, would learn to avoid the sound.

3. The warning serves to conserve venom and fangs, also an advantage to the snake.

4. Some of the other uses for the rattle which have been suggested are inconsistent with rattler habits; others are possible, but there is little field evidence to validate them, and such as there is, may be subject to alternative interpretations.

5. Experiments by one investigator indicate that rattlers cannot hear the sound of the rattle; if verified, these at once eliminate any theories such as the mating-call, call-for-help, and other uses dependent on an exchange of signals between snakes.

6. The rattle vibration is at too high a frequency to permit recognition of discrete sounds. It is a hiss rather than a rattle. Certain species of cicada or the hiss of a small jet of steam most closely approximate the sound of the rattle.

7. The rattle is operated by transverse vibrations of an amplitude of a millimeter or so, produced by six muscles in the tail. Viewed under stroboscopic light, the vibration is seen to have the effect of sending transverse waves out to the end of the rattle string. Because of a cumulative looseness of interlock, the waves enlarge as they progress outward. Analysis shows the vibration to approximate simple harmonic motion.

8. The sound is produced principally by the striking of the adjacent segments against the inner and outer surfaces of the anterior transverse groove.

9. As determined by kymograph records, the speed of vibration depends more on temperature than any other single factor. There probably are species differences but they have not been definitely determined. Frequencies of from 28 to 67 cycles per second were noted. A speed of about 48 cycles is normal at about 65° F.

10. The loss of rattles to maintain the string at

from 5 to 9 segments is normal and beneficial, since very long strings are inefficient vibrators. Strings above 14 segments are quite exceptional.

11. The more placid species tend to have longer strings; the same is true of snakes which live in areas where enemies are infrequent or absent, as is the case with certain island forms. Snakes in rocky or brushy country have shorter strings than those which live in sandy areas. The larger species tend to have longer strings, on the average, than the smaller. The first rattles acquired are the most fragile and hence the longest strings seldom are unbroken strings.

12. Gross chemical analyses are given. The composition of the rattle is not greatly different from that of the snake skin.

13. The prebutton, or rattle with which the snake is born, is always lost with the first shedding, which usually takes place within a week or two after birth. The prebutton, by its structure, gives important clues to the genesis of the rattle.

14. The probable interrelation between the rattle and the skin is discussed. While the rattle is analogous to a scale top, it has widely differentiated therefrom. It is laid down as a lamellate clay-like substance, on a basal matrix of tissue which gives it its shape. Later it hardens, becomes transparent, and springs away from the matrix. The anterior edge is not joined to the skin, from which it is sharply differentiated. The rattle is deposited on the skin of the matrix, which is coördinated with the skin of the body.

15. While some observers have doubted the synchronism of rattle acquisitions with skin changes, it is thought that they were misled by the erratic character of exuviation in captive specimens. The nature of the process would seem to indicate an absolute synchronism in normal growth. Probably most species add from three to five rattles per year. This may be reduced when the adult size is attained and growth is slower.

16. Increments in rattle size are rapid up to, and including, rattle No. 6, but slower thereafter, although apparent up to rattle No. 12 or 14. Subsequently, individual variations and seasonal fluctuations mask growth; the sides of the string become substantially parallel.

17. The rattle-shifting mechanism, whereby the first and second lobes of each rattle grip the second and third lobes of its successor, without affording any opportunity for the string to drop off, is quite intricate. It is effected through a wave action of the matrix, whereby the lobes of tissue move backward (relative to the skin and vertebrae) and gradually decrease in size by exudation. The same element of matrix skin deposits a corresponding element of each rattle, so that a defect, if one be present, always reappears on each rattle at the same point.

18. Structurally, the rattle is of beautiful and intricate design, reinforced at possible points of weakness; for example, there is a fold where a tear might start at the anterior edge, the sides are furrowed for reinforcement, and

strengthening webs appear in the transverse grooves. Successive segments are separated with difficulty.

19. A longitudinal asymmetry is present and is important for two reasons: It prevents the end of the rattle from dragging; and it holds the rattle in a straight line, instead of permitting it to drop in a curve, when it is balanced in the rattling position. The latter is at an angle of about 10 degrees from the vertical; in this position of balance the greatest efficiency--maximum sound with least wear--is attained. The asymmetry is produced by a curve in each rattle segment and a tighter fit, between interlocking lobes, in the upper half of each segment as compared to the lower.

20. A typical rattle is described. Three lobes per segment are normal in the adult, but four lobes are occasionally found.

21. Species differences in rattle color and lobe conformation are discussed; also in matrix color, which is really a part of body pattern. This paper omits discussion of interspecific variations of rattle dimensions, a phase of the investigation scheduled for subsequent publication.

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